

**FLORAL COLOR ASSEMBLY OF SERPENTINE SEEP COMMUNITIES IN  
NORTHERN CALIFORNIA, USA**

by

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Species traits, particularly those that impact fitness, can shape the evolutionary relationships among coexisting species. Trait distribution (underdispersion, overdispersion) within communities can provide evidence of key ecological interactions (e.g., competition, facilitation) that can contribute to assembly. The distribution of floral colors in a community may reflect pollinator-mediated interactions, and the phylogenetic distribution of color can also affect inferences of ecological mechanisms at play. Additionally, the scale of local habitat may influence the type or strength of ecological interactions among co-occurring species. I examined how floral color is distributed within replicated co-flowering assemblages with the use of pollinator color vision models. Incorporating these biologically relevant models into the study of floral color assembly processes is relatively new and untested for an entire co-flowering community with generalist pollinators. I modeled floral spectra of 55 co-flowering species through honeybee and syrphid fly color vision to assess color trait structure across 14 serpentine seep communities in California. I then compared our findings to null model predictions. We asked: is there evidence for nonrandom distribution of floral color in the community? Is there phylogenetic signal for floral color? If so, is there phylogenetic underdispersion or overdispersion across local communities? Is there an effect of habitat scale on these outcomes? I found that the observed color assemblage is not due to any phylogenetic history, and there is no

phylogenetic signal for the selected floral color metric. I found a significant negative relationship between habitat scale and trait dispersion. Competitive exclusion could be a dominant interaction outcome at small scales, but it is less detectable/unimportant at larger scales.

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## PREFACE

“You can never tell with bees.”

- Winnie the Pooh, from *Winnie the Pooh and the Honey Tree* (1966)

This journey of discovering new insights into cognitive pollination ecology could not have been possible without many wonderful folks. I would like to acknowledge my fellow students George Meindl, Matthew Koski, Gerardo Arceo-Gomez, and Nicole Forrester for their helpful comments and encouragement. George and Gerardo both provided me with several floral color samples that have contributed to this research. Matthew started the preliminary exploration of floral color collection for our lab, and I am grateful for this groundwork that Matthew laid. I would like to thank Paul Aigner and Catherine Koehler of the UC Davis McLaughlin Natural Reserve for help with plant identification and transportation, Rachel Germain for thoughtful comments, and Riley B. Spahn for assistance in developing code for the null model analyses in Python. I am grateful to have received a National Science Foundation Graduate Research Fellowship Program award that has supported this work and my development as a scientist. Additionally, I am thankful for Assistant Professor Dr. Nathan Morehouse for carefully training me in color sample collection, introducing me to insect color vision modeling, and Dr. Morehouse was instrumental in the intellectual development of this project. I would like to acknowledge Dr. Tia-Lynn Ashman, Dr. Susan Kalisz, Dr. Jonathan Pruitt, and Dr. Stephen Tonsor for all of their encouragement and collective feedback on my work. Lastly, I would like

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## **1.0 INTRODUCTION**

In his published MacArthur Award Lecture in 1992, Simon Levin argued that science's essence is "understanding patterns in terms of the processes that produce them (1992)." In a rapidly changing world threatened with major losses of biodiversity and ecosystem function (Mori et al. 2013), ecologists must seek to elucidate the mechanisms that generate and sustain variation in observed patterns of co-occurring species or trait assemblages (Diamond 1975). The presence of an organism in an observed community may be contingent upon their phenotype (behavioral and physical) in relation to the abundance, diverse assortment, and identity of phenotypes expressed by other organisms present in the assemblage (Webb et al. 2002, Cavender-Bares et al. 2009). Recent advances community assembly studies have integrated the importance of relatedness among taxa in communities and thereby have been able to make predictions as to what ecological processes are shaping community patterns (Cavender-Bares et al. 2006, Herrera et al. 2010).

With the consideration that recently diverged species are often ecologically similar (Darwin 1859), the evolutionary relatedness of co-occurring community members is highly relevant to understanding the extent of phenotypic diversity and abundance that exists (Kraft et al. 2007, Cavender-Bares et al. 2009). This phenomenon of closely related taxa exhibiting ecological similarity has been documented across many traits, and it is referred to as phylogenetic signal (Blomberg et al. 2003). By incorporating these three pieces of information --

trait community structure, phylogenetic community structure, and phylogenetic signal of the trait in question – we can begin to elucidate the ecological mechanisms that provide the observed phenotypic and phylogenetic patterns we see in communities.

Possible ecological mechanisms that can shape community patterns include biotic mechanisms such as competition and facilitation (Webb et al. 2002), abiotic mechanisms including habitat filtration (Ackerly 2003), and neutral assembly (Hubbell 2001). Competitive interactions can produce phenotypically overdispersed communities, whereby co-occurring species are more different from each other than chance would predict (Cavender-Bares et al. 2009). The actual mechanism of differentiation can occur different manners: either ecological sorting occurs among co-occurring taxa with overlapping niches, to the effect that one or more species is excluded from the community (Peay et al. 2011), or character displacement occurs, where co-occurring species have evolutionarily diverged from their original phenotypes to minimize interspecific competition and thus coexist (Armbruster et al. 1994). Communities shaped by competitive interactions will have overdispersed phenotypes, and if there is phylogenetic signal for the phenotype, there will be phylogenetic overdispersion, too. Competitive interactions are the most common biotic ecological interaction found in community assembly studies (Kraft 2007).

Ecological facilitation, whereby the presence of at least one species benefits at least one other species is thought to produce phylogenetic clustering, or underdispersion, but it has been rarely documented (Sargent and Ackerly 2008). Abiotic habitat filtration occurs when the habitat in which species co-occur selects for community membership, where only species with suitable traits (such as drought tolerance or heavy metal tolerance) can thrive in the environment. If the trait of interest is phylogenetically conserved, habitat filtration will produce phenotypic

underdispersion in communities (Webb et al. 2002). Random assembly, in part due to demographic stochasticity and limited dispersal, will show no under- or overdispersion in community structure: there will be no community structure in respect to the traits of interest (Hubbell 2001).

The influence of any ecological mechanism on trait distribution may vary across spatial scale (Levin 1992). It has been found that when studying a phylogenetically conserved trait across a community, different ecological mechanisms are thought to be responsible for patterns of phylogenetic dispersion with changing spatial scale (Cavender-Bares et al. 2006, Kembel and Hubbell 2006). Biotic mechanisms, such as competition and facilitation, are considered to operate at small spatial scales, whereas abiotic habitat filtration operates at larger spatial scales (Cavender-Bares et al. 2006). However, not all traits are evolutionarily conserved, so there is a need to understand if we can identify trait patterning in the same manner: trait underdispersion or overdispersion may also be due to differences in the shifting dominance from biotic mechanisms to abiotic mechanisms with increasing spatial scale, regardless of phylogenetic signal or phylogenetic community structure (Arista et al. 2013). Our questions were: 1a) is there underdispersion or overdispersion of a given functional trait in observed communities? 1b) Is there an effect of community scale and size on dispersion patterning? 2) Is there trait structuring even with random phylogenetic structure and lack of phylogenetic signal?

An ideal study system to address this gap in knowledge of community assembly is one with a strong body of literature documenting ecological interactions affecting traits of particular interest. One area of study that easily meets these conditions is that of flower color diversity. Spanning the entirety of the ultraviolet and visual color spectrum, flowers are able to send signals with such a diversity of color because of the variation in tissue cellular structures and

pigment production (Grotewold 2006). The diversity of floral color even between sister species is a remarkable example of a highly evolutionarily labile trait (Rausher 2008). Pollinator-mediated selection is thought to drive transitions in floral color. One historical theory regarding floral color change is the pollinator shift model, which simply states shifts in dominant pollinators of flowers contributed to floral color radiation (Ollerton et al. 2009), but recent findings have shown that a number of floral radiations with highly diverse coloration did not undergo pollinator shifts (Cooley and Willis 2009).

The floral color diversity of a community of co-flowering plant species may be shaped by other factors, particularly their co-flowering neighbors and pollinators (Sargent and Ackerly 2008, Ghazoul 2006, Schiestl and Johnson 2013). These ecological mechanisms may be biotic or abiotic. Examples of biotic mechanisms shaping floral color assembly include competition (such as co-flowering plants competing for pollinators, selection can drive competitive exclusion). An example would be that of a highly diverse floral color present in a co-flowering assembly would enhance pollinator fidelity, increase pollinator constancy (Chittka 1997, Gumbert et al. 1999, McEwen and Vamosi 2010, Muchhala et al. 2014). Alternatively, facilitation (Bruno et al. 2003, Rathcke 1983) may occur where one or more co-flowering species enhances a different species' reproductive success. An appropriate example involves one (or both) species enhancing pollinator visitation to the other species due to their high similarity in floral color, which can enhance perceived floral abundance for pollinators (more so than a single species could produce alone). Competition has been documented far more frequently than facilitative outcomes (Muchala et al. 2014). Facilitation could be potentially hard to detect in part because of conflicting problems with increased HPT, and density-dependent contexts of pollen load purity (Hanoteaux et al. 2013, Hegland and Totland 2012, Feldman et al. 2004, Rathcke 1983).

Abiotic ecological mechanisms include habitat filtration. In habitat filtration, the habitat in which species co-occur selects for community membership, where only species with suitable traits for survival can thrive in this environment. The strength of pollinator-mediated selection of floral color may be much weaker compared to the overall climate factors driving filtration of species with random assemblages of floral color (Sargent and Ackerly 2008). Pollinators have been thought to be part of the “habitat filtration” factors, where the presence or absence of a given pollinator would influence the presence of a floral color (example: if hummingbirds aren’t present, species with red flowers/ red flower morphs would experience low reproductive success/local extinction) (Campbell et al. 2012, Sargent and Ackerly 2008) However, in a pollination community with nestedness, or many generalist-pollinated plant species, pollinators may not actually be a strong filtering force (Sahli and Conner 2006).

There is a developing body of literature using our understanding of pollinator vision to study the distribution of floral color in communities (Binkenstein et al. 2013, de Jager et al. 2011, Muchhala et al. 2014). Incorporating cognitive pollination ecology into community ecology is an important step forward in assessing the importance of pollinator-mediated selection of flowering plant communities (Leonard and Masek 2014, Schiestl and Johnson 2013). Having a distinct/different flower color signal in a co-flowering community is thought to be advantageous for increased pollinator fidelity and decreased HPT (Waser 1983, Kevan 1978) and less instances of hybridization (Levin 1971, Tastard et al. 2012) Floral color is in part coded for insect vision, but also constrained biochemically and phylogenetically (van der Niet and Johnson 2012). We do not know how important pollinator discrimination capabilities are in the assembly floral color (Chittka 1997, Devaux et al. 2014).

## **2.0 METHODS**

### **2.1 STUDY SITE**

We selected 14 serpentine seeps at McLaughlin Natural Reserve for study. Seeps are tributaries of creeks and are characterized by the water that flows slightly below the ground surface, creating a wet soil environment for much of the dry season in northern California. Serpentine soil is characterized by a high magnesium to calcium ratio and contains many heavy metals. The serpentine plant community is uniquely adapted to thriving and/or tolerating this soil that is generally toxic to all other plants (Harrison and Rajakaruna 2011). Seeps were picked to represent a range of sizes, from 0.04 km<sup>2</sup> – 0.55 km<sup>2</sup>. On average, seeps were located 4.24 km apart from one another. Plant species were included for this study based on our surveys performed in the seeps and adjacent grassland in 2010, 2011, and 2013. These species are known to co-occur and co-flower.

### **2.2 POLLINATOR VISITATION SURVEYS**

Pollinators were recorded to visit the flowers of as many focal seep species as possible in 2010, 2011, and 2013. Visitors of interest were categorized in functional groups of “bees” and “flies”. If pollination could not be observed for a given species for any reason, we incorporated



knowledge cited in scientific literature about the pollination ecology of each species. From these data we then were able to note if bees and/or flies were primary visitors to a given species. After three years of pollinator surveys in the field, an extensive search of pollination literature, and accessible natural history accounts, there were three plant species remaining for which we had no pollinator information that were documented in at least one seep (*Acemisson americanus*, *Hesperolinon californicum*, and *Hoita machrostachya*).

### 2.3 SITE SURVEY

Site surveys were performed once for each site in the peak flowering times of June and July of 2013. Seep length, average width, whole plant density, and species number were recorded as metrics for seep habitat size and diversity. At each site, a transect line was laid along the longest axis of each seep. Along this line, the tape was placed in the middle of the seep. At every 0.25m of the transect tape, it was documented whether the transect tape at that point was over bare ground (soil or rock) or in contact with a plant. If transect tape was in contact with a plant, the plant was identified to species and it was noted whether it was in flower, withered/dried, or only in vegetative form. Additionally, to survey adjacent grassland, a transect line was run on the east or south side of the seep (depending on how the longer axis of the seep was oriented), and it was surveyed in the same manner as the seep transect line. Each site was surveyed in this manner for up to 100m. If seep was longer than 100m, then 50m of the survey was conducted at the ends of the longest axis of the seep (25m at each end) and 50m of the survey were conducted in the middle of the seep. The width of the seep was measured haphazardly at five different points to find average width of seep.

## 2.4 COLOR COLLECTION

Of 63 regional co-flowering species present in seeps or directly adjacent to seeps from three years of field observations, the color of 55 co-flowering species were collected (table 1). We were able to collect floral color measurement samples from five different individual plants for 45 species. We were able to collect floral color measurements from four different individual plants for 1 species, *Plagiobothrys stipitatus*, three different individual plants for 3 species (*Acmispon parviflorus*, *Allium amplexans*, *Antirrhinum cornutum*), two measurements from different individual plants for *Hesperolinon disjunctum* and *Mimulus layneae*., and we were able to collect floral color measurements from one individual plant for four species: *Heterocodon rariflorum*, *Lagophylla minor*, *Sisyrinchium bellum*, and *Collinsia sparsiflora*. The remaining eight species could not be measured for color. All of these eight species have been documented as sporadic and infrequent in the seep communities and their surrounding grassland habitats, with single flower counts in a given seep at any time. Two of the species are taxonomically difficult to distinguish past genus, and two of the species were documented as flowering in 2010 and 2011, but not 2013, and when flowering, they were never observed being visited by pollinators. We excluded these eight species for community trait analysis, community phylogenetic analysis, and testing for phylogenetic signal.

Spectrometry was used to collect color samples from flowers haphazardly sampled from different individual plants from fourteen seeps using an Ocean Optics Spectrometer. A deuterium-halogen light source was used with an OceanOptics white standard to measure percent transmission from 300-700 nanometers, which is the general range of color perception by many pollinators, including bees and flies. A single petal was measured for each flower, or in the

instance that petals were too small, multiple petals were overlaid to provide enough surface for the spectrometer to collect a reflectance reading (McEwen and Vamosi 2010).

One to five individual flowers from different individuals for each species were measured for reflectance readings, haphazardly selected from within the fourteen seeps sampled. By viewing the spectral reflectance curves of samples for three focal species (one common, one with internal contrast, and one rare species), we found no variation in species reflectance between seeps. We found repeatability in our spectral readings for single individual flowers for two other haphazardly selected species' samples, one species that has large petals ( $R^2$ : .99967, *Thermopsis macrophylla*), and one species that required overlaying multiple petals for reflectance reading ( $R^2$ : .90365, *Sambucus mexicana*).

For each individual flower, reflectance readings were obtained from various portions of the floral surface, particularly if there was a noticeable change in coloration in the human vision color spectrum or morphological component (e.g.: petal v. labellum), but we also searched for any change in the ultraviolet reflectance range across the floral display area. These multiple reflectance readings for a single flower were then weighted by their proportion of its representative measured floral area. This proportion was estimated by searching for distinct changes in UV spectral reflectance along the surface of the flower using the spectrometer (when considering UV internal contrast), and the percent area for each different color in human color perception was also roughly estimated by eye. The weighted spectral reflectances were then averaged together to create one reflectance reading for a given individual. This average was calculated for all individuals, and then each average for an individual of a species were averaged together to represent a spectral reflectance of that single species. If the species did not show internal contrast in reflectance readings, the reflectance readings for each individual flower were

averaged together to represent a single species. All reflectance readings were binned into 1nm increments between 300-700nm

Irradiance data was collected using an OceanOptics Jaz Spectrometer in the field during midday. This measurement of irradiance is used to represent the irradiance of the co-flowering season, and it is an important piece of information used when calculating the trait value with pollinator vision modeling. The calculation uses the irradiance as a “background” standard of ambient light in the field.

**Table 1.** List of 55 plant species used in study, along with community membership and pollinator visitation information. Seep sites are ordered 1-14 with increasing species number. An X in the “F” Visit column denotes that a focal plant species is visited by fly species, an X in the “B” Visit column denotes that a focal plant species is visited by bee species.

	Visit		Seep Sites													
Plant Species Name	F	B	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Allium amplexans</i>	X	X														
<i>Anagallis arvensis</i>	X	X					X					X				
<i>Antirrhinum cornutum</i>		X			X	X			X	X	X		X	X	X	X
<i>Angelica tomentosa</i>	X							X								
<i>Aquilegia eximia</i>								X						X		X
<i>Astragalus clevelandii</i>	X	X					X	X				X		X		X
<i>Brodiaea elegans</i>	X	X							X	X						
<i>Calochortus amabilis</i>	X	X														
<i>Castilleja foliolosa</i>				X		X				X	X	X	X			X
<i>Calycanthus occidentalis</i>																
<i>Calystegia purpurata</i>																
<i>Castilleja rubicundula</i>	X	X					X								X	
<i>Centaurea solstitialis</i>		X					X	X						X		
<i>Zeltnera trichantha</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Clarkia gracilis</i>		X				X			X	X	X		X		X	X
<i>Collinsia sparsiflora</i>		X														
<i>Delphinium uliginosum</i>	X	X			X	X	X		X	X		X			X	X
<i>Epipactis gigantea</i>	X															
<i>Eriophyllum lanatum</i>	X	X									X				X	X
<i>Eschscholzia californica</i>		X							X	X						

	Visit		Seep Sites													
Plant Species Name	F	B	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Grindelia hirsutula</i>	X	X							X			X				
<i>Helenium bigelovii</i>		X	X					X								
<i>Hesperolinon californicum</i>										X						
<i>Hemizonia congesta</i>	X					X			X			X			X	
<i>Hesperolinon disjunctum</i>	X	X														
<i>Helianthus exilis</i>		X			X	X	X		X	X	X	X	X	X	X	X
<i>Heterocodon rariflorum</i>		X														
<i>Horkelia californica</i>		X											X			
<i>Hoita macrostachya</i>								X					X	X		
<i>Lagophylla minor</i>		X													X	
<i>Lessingia micradenia</i>		X				X				X	X	X		X	X	X
<i>Acmispon brachycarpus</i>		X														
<i>Acmispon parviflorus</i>		X														
<i>Acmispon americanus</i>				X			X		X	X	X			X	X	X
<i>Mimulus guttatus</i>	X	X			X	X	X	X	X	X	X	X	X	X	X	X
<i>Mimulus layneae</i>	X	X									X				X	
<i>Mimulus nudatus</i>	X	X									X		X	X	X	X
<i>Monardella viridis</i>																
<i>Penstemon heterophyllus</i>								X								
<i>Plagiobothrys stipitatus</i>	X	X		X									X	X	X	X
<i>Ranunculus californicus</i>	X	X														
<i>Rhododendron occidentale</i>		X														
<i>Sambucus mexicana</i>		X														
<i>Scutellaria siphocampyloides</i>	X	X							X			X	X	X	X	X
<i>Packera clevelandii</i>		X	X	X				X			X		X	X		X
<i>Sisyrinchium bellum</i>		X														
<i>Sidalcea diploscypha</i>		X										X				
<i>Solidago californica</i>	X	X					X						X			X
<i>Stachys albens</i>		X		X				X				X	X	X		
<i>Streptanthus brachiatus</i>		X	X							X	X					
<i>Thermopsis macrophylla</i>													X			
<i>Trichostema laxum</i>		X	X	X	X	X	X	X	X	X	X	X	X	X		X
<i>Trifolium obtusiflorum</i>	X	X						X							X	
<i>Triteleia peduncularis</i>	X	X	X		X	X		X	X	X	X	X	X	X	X	X
<i>Toxicoscordion venenosum</i>	X	X			X			X	X	X	X	X		X	X	X

### 3.0 ANALYSES

#### 3.1 POLLINATOR VISION MODELING

We used mathematical models of color vision for representative bee (*Apis mellifera*) and fly (*Eristalis tenax*) pollinators. Bees and syrphid flies generally have three color photoreceptor types: ultraviolet (UV), blue (B) and green (G) (Peitsch et al. 1992). Our model of color vision uses “color opponency” which is the interpretation of the relative amounts of light captured by each photoreceptor type into a perceived color. Using the known photoreceptor sensitivities of the insect across each wavelength of light, we were able to measure the quantum catch of each photoreceptor type:

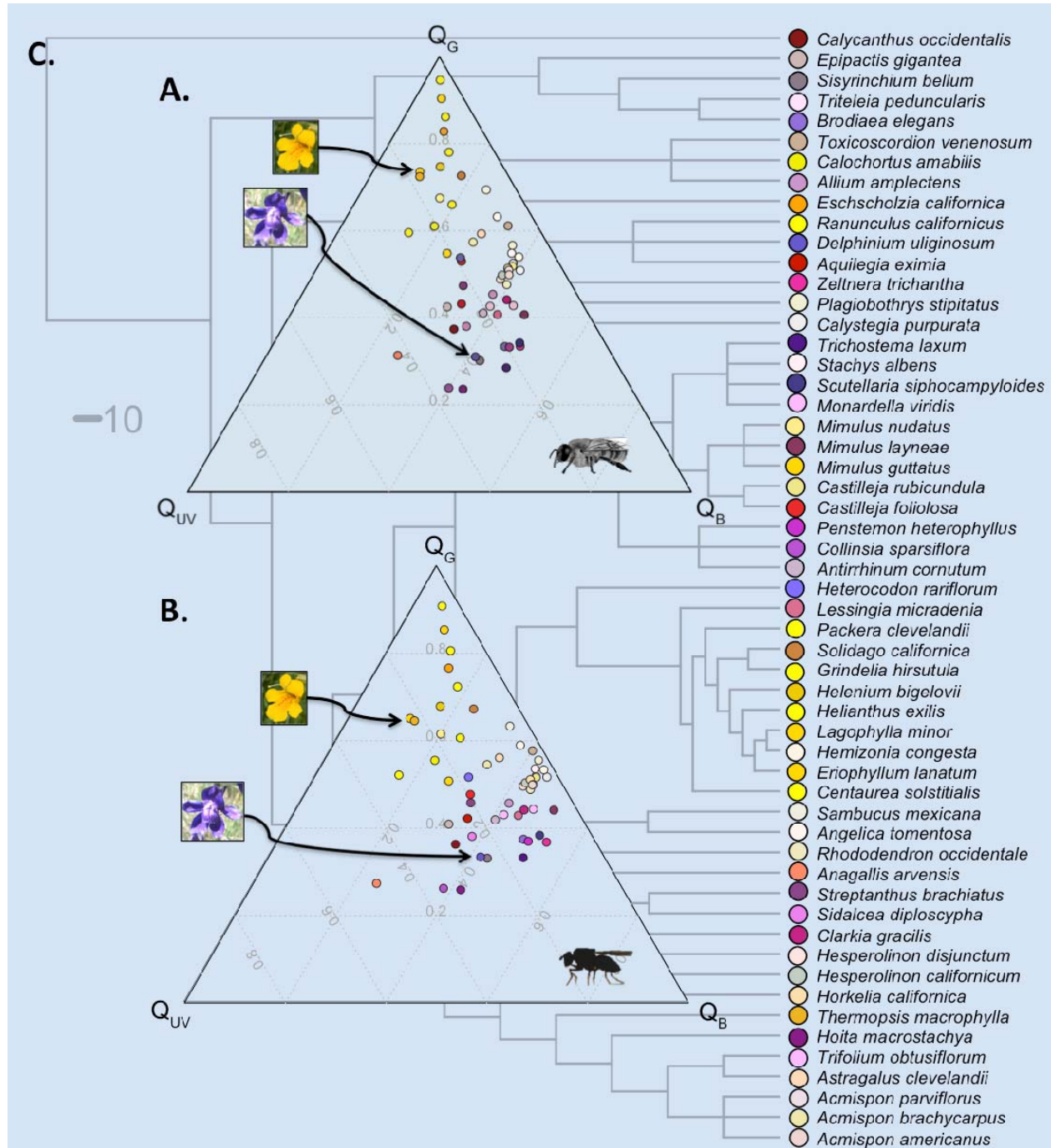
$$q_i = Q_i / (\text{sum}(Q_i)),$$

where  $Q_i = \int_{\lambda} R_i(\lambda) S(\lambda) I(\lambda) d\lambda.$

where  $q_i$  represents each photoreceptor type. In the second equation,  $\lambda$  is the wavelength,  $R_i(\lambda)$  is the spectral sensitivity of the photoreceptor,  $S(\lambda)$  is the spectral reflectance of the surface (the floral tissue), and  $I(\lambda)$  is the spectral irradiance of the illuminant (the light environment). We then mapped these relative quantum catches of each photoreceptor (for 55 flowering species) onto a chromaticity map. Because our bee and fly model have three color photoreceptor types, the chromaticity map values can be visualized as a ternary/triangle plot, with a single dot

representing a single plant species in color space (Fig. 1a & 1b). The distance between any two dots on the chromaticity map represents the discriminability of the insect to distinguish the two different color signals. Vorobyev and Osorio (1998) stated that one must incorporate elements of photoreceptor “noise” and relative photoreceptor densities to get a clearer understanding of discriminability. We modeled the pairwise differential stimulation for each flowering species combination, and the units were converted to “just noticeable differences” (JNDs) or  $\Delta S$  values. These  $\Delta S$  values are a behavioral predictor for whether or not the insect can cognitively discriminate between the selected pair of focal stimuli (Vorobyev and Osorio 1998).  $\Delta S$  has been significantly tested in *Apis mellifera* with reliable success in predicting behavior, and  $\Delta S$  is used with other pollinators’ model systems as an estimate of pollinator foraging choice (Hempel de Ibarra et al. 2014).

In order to calculate this pollinator vision metric, the program AVICOL was used. AVICOL uses a honeybee vision model, which is a representative vision system, (Kaczorowski et al. 2012, Leonard and Papaj 2011), as well as a fly vision model, because flies were the second-most common flower visitors to the plant community.



**Figure 1.** Ternary plots of focal pollinator color vision across the angiosperm phylogeny. 1A. Ternary plot of the differential stimulation of color photoreceptor types of *Apis mellifera*. 1B. Ternary plot of the differential stimulation of color photoreceptor types of *Eristalis tenax*. 1C. Phylogenetic tree of co-flowering seep community. Colored circles next to tips represent the color of the flower as seen by the human eye and match the dots presented



in the ternary plot. When 1C. is compared with 1A. and 1B., the  $Q_{UV}$  corner of each ternary plot differentiates the visual wavelength spectrum from ultraviolet coloration.

### **3.2 PHYLOGENETIC TREE CONSTRUCTION**

An ultrametric phylogenetic tree of the regional species pool was generated including all species for which color was collected (Fig. 1c). This was done by using Phylomatic 3.0 and Phylocom 4.2, which incorporated known branch lengths from Wikström and others using the BLADJ function in Phylocom (2001).

### **3.3 PHYLOGENETIC SIGNAL ANALYSES**

Because the trait of interest  $\Delta S$  is a multidimensional trait, common and tested methods of calculating phylogenetic signal cannot be used as they generally test for the signal of one-dimensional traits. According to , the acceptable course of action with a multidimensional trait is to test for phylogenetic signal by performing Mantel tests, which used a pairwise  $\Delta S$  trait distance matrix and tested for any correlation with a phylogenetic distance matrix of mean phylogenetic distances (MPDs) for each of the seeps. This Mean Pairwise Distance is defined as the mean phylogenetic distance between two random species within a defined species pool (i.e., seep) created by Phylocom 4.0 using the 'comstruct' function.

### **3.4 PHYLOGENETIC COMMUNITY STRUCTURE ANALYSES**

To find evidence for distinct patterns of phylogenetic community structure, we calculated the observed mean phylogenetic distances (MPDs) for each of the seeps. This observed metric was compared against the mean MPD measured from 10,000 random null communities generated for each seep, keeping seep species richness the same but generating communities with random species from the regional species pool. In effect, this function generates 10,000 random communities and compares the mean pairwise phylogenetic distances for each random community to the observed community. This was done for each seep community, keeping species richness the same for each null model for each respective observed seep (for a total of 14 seeps). To see if phylogenetic community structure is related to seep size, diversity, and plant density, I performed an ANCOVA of the data generated by phylocom (particularly, the observed MPD and the null model MPD for each seep) and used the first Principal component of a PCA combining seep area, seep species number, and seep whole plant density measurements. This PC1 explained 75% of the variation in data. Negative loadings of PC1 indicated small seep communities in area, whole plant density, and species number, whereas positive loadings of PC1 referred to larger, more dense, and species-rich seep communities.

### **3.5 TRAIT COMMUNITY STRUCTURE ANALYSES**

To find evidence of any nonrandom pattern of trait community structure, we first created a Python code using NumPy that matched pairwise  $\Delta S$  values of all species for each of the seeps, with respect to the observed species richness of each observed seep. With this set richness

parameter, a null model generated 10,000 random null communities for each seep, with random species drawn from the regional species pool without replacement within a single iteration. We performed these calculations for the bee and fly vision system including all plant species, and then we ran different analyses after filtering out the plant species that the bee or the fly was not recorded to visit. To see if trait community structure is related to seep size/diversity, we ran an ANCOVA of the data generated by python (the observed trait variances vs. the null model trait variances for each seep) and used PC1 of seep size, density, and species number to determine if and how seep size/diversity was related to any change in the observed trait variance in a community. This was performed in SAS 9.4. The response variable for the ANCOVA is  $\Delta S$ . The main effect is the first principal component of species richness, whole plant density, and seep area.

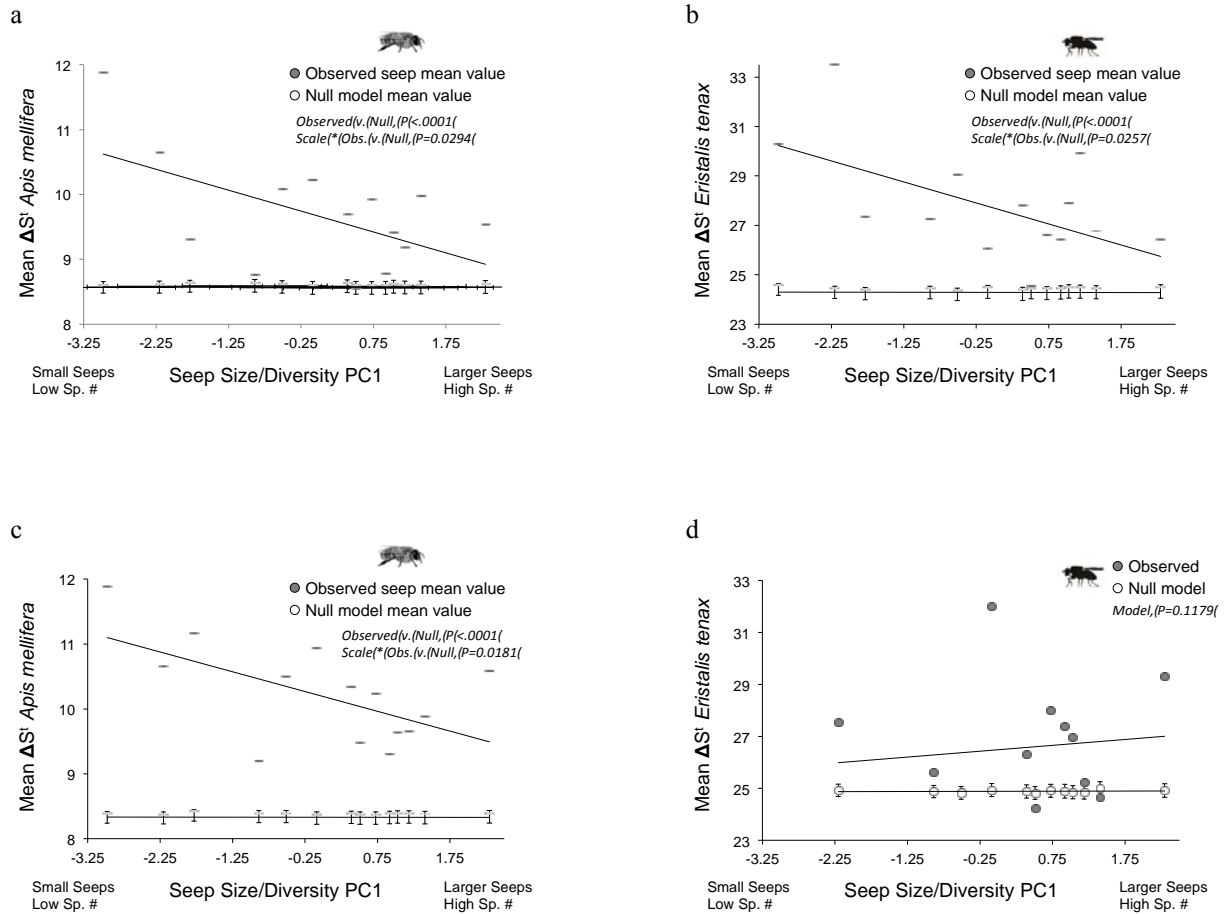
## 4.0 RESULTS

### 4.1 TRAIT COMMUNITY STRUCTURE

When all selected co-flowering species (regardless of insect visitation status) were modeled through bee and fly color vision models, all observed seep communities were overdispersed and significantly more discriminable compared to null model predictions (bee model: GLM  $F(3,24)=13.52$ ,  $p < .0001$ , observed v. random  $F(3,24)=29.72$   $p < .0001$ , fly model: GLM  $F(3,24)=18.35$ ,  $p < .0001$ , observed v. random  $F(3,24)=43.62$ ,  $p < .0001$ ) (Fig. 2a-b). Additionally, in each analysis there was a significant interaction term with a negative relationship of mean observed seep  $\Delta S$  and PC1 of seep habitat size/diversity (bee: interaction term  $F(3,24) = 5.37$ ,  $p = 0.0294$ , fly: interaction term  $F(3,24) = 5.66$ ,  $p = 0.0257$ ).

For models that were run respective to the visitor-specific species pool, the bee model described the observed mean seep  $\Delta S$  values were still significantly overdispersed compared to null model predictions, and there was still a significant negative relationship between  $\Delta S$  and PC1 of habitat size/diversity (bee-specific model: GLM  $F(3,24)=42.66$ ,  $p < .0001$ ; observed v. random  $F(3,24)=115.00$ ,  $p < .0001$ ) (Fig. 2c). However, with the fly model, the two seep communities with the lowest species richness had to be removed from the analysis because only two of the species in each of the observed seeps were known to be visited by flies. After

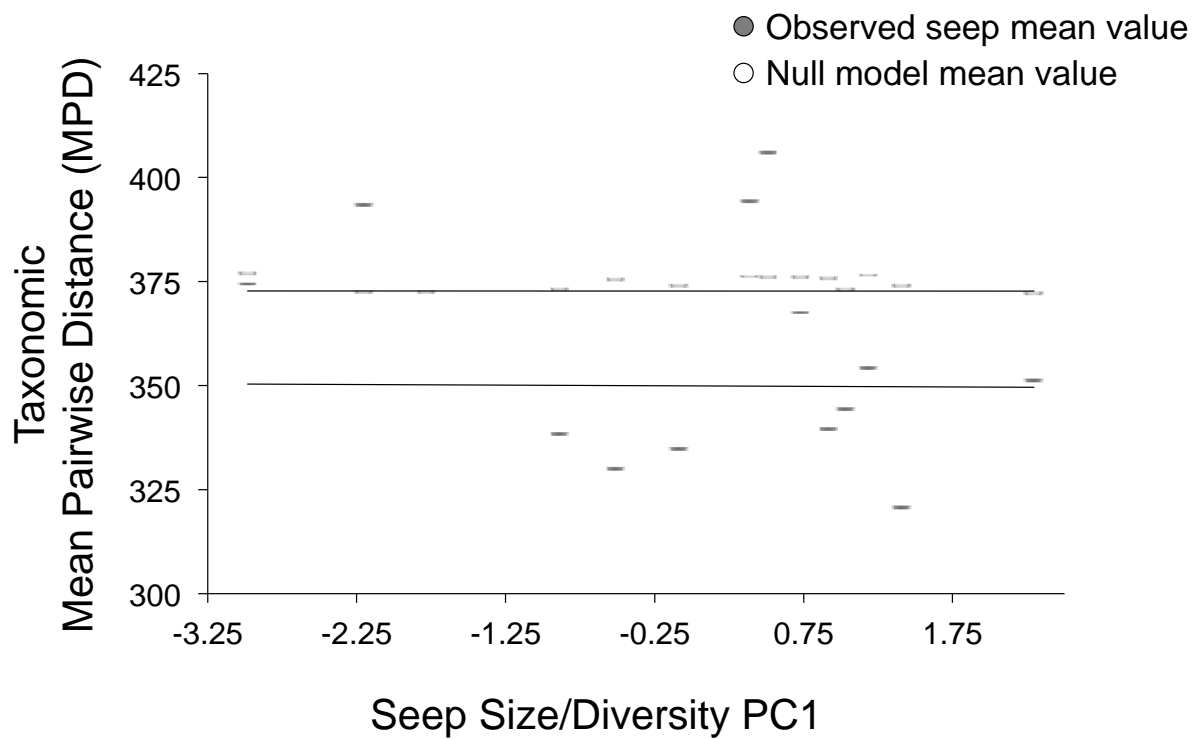
removing those two observed and respective null values, the model was not significant (fly-specific model: GLM  $F(3,22)=2.19$ ,  $p=.1179$ ) (Fig. 2d).



**Figure 2.** Comparison of observed and null mean  $\Delta S$  values across PC1 of seep size/diversity. Low PC1 values refer to small seeps with low species richness, high PC1 values correspond to large seeps with high species richness. Error bars present on null mean  $\Delta S$  values represent 95% Confidence Intervals. a. all co-flowering species modeled through bee vision system. b. all co-flowering species modeled through fly vision system. c. species not found to be visited by bees have been removed from this analysis d. species not found to be visited by flies have been removed from this analysis.

## 4.2 PHYLOGENETIC STRUCTURE AND SIGNAL

There was no phylogenetic community structure detected over the observed seep communities; and there was no relationship between habitat size/diversity and phylogenetic relatedness (GLM model  $F_{3,24} = 1.91$ ,  $P > 0.1$ ) (Fig. 3). The Mantel tests conducted for phylogenetic correlations with bee or fly  $\Delta S$  values were highly insignificant, each reporting at  $P > 0.5$ .



**Figure 3.** Comparison of observed and null Mean Phylogenetic Distances (MPDs) across seep size/diversity scale.

## 5.0 DISCUSSION & CONCLUSIONS

Because we failed to find nonrandom phylogenetic community structure and phylogenetic signal of floral color, the observed trait assemblages (overdispersed  $\Delta S$  for three of the four models) are not due to any phylogenetic history. This supports our claim that an ecological mechanism is structuring the observed seep communities to where they are very easy to tell apart through the eyes of a pollinator. These patterns of overdispersion are consistent with patterns of competitive exclusion/limiting similarity processes. Our findings are consistent with previous studies. Muchala and others (2014) also found evidence for competitive exclusion in pollinator color vision space. Their community assembly study focused on one genus, however, whereas our analysis covered an entire co-flowering assemblage.

The fly-specific visitor model was not significant in its analysis, and this may be due to decreased statistical power after removing two seep communities, or it could indicate that flies are not as strong in selective pressures on color structure as bees appear to be in this pollination community. Further work in the field should be done to measure reproductive success of different co-flowering species with experimental manipulations of pollinator exclusion, bees only, flies only, or both pollinators in pollination assays.

Additionally, there is a significant negative relationship between habitat scale and trait dispersion, to where overdispersion decreases with increasing seep size and diversity. This could mean that competitive exclusion is a dominant interaction outcome at small scales, but this

assembly mechanism is less detectable at larger scales. The lack of detection could be due to other ecological mechanisms drowning out competitive signals at larger seep scales.

Color vision system modeling is a rapidly growing field, and with the addition of new vision models and their application for closely related species of each model system, we must continue to rigorously test the functional relevance of these estimators of discriminability (Hempel de Ibarra 2014). We must recognize the limitations of focusing intensely on only one metric of one sensory pathway of a pollinator: by not considering the role of other important components (e.g., olfactory cues, flower display size, floral reward composition) we are limited in our ability to estimate the entire story of how a community collectively attracts pollinators and their species interactions.

Further work should be done to calculate species turnover in focal seep communities to confirm that these assemblages are consistent in pattern. Because these serpentine seeps can be visualized as islands, we can also incorporate our knowledge of general Island Biogeography Theory to our predictions. Knowing that larger habitats have higher species colonization to extinction ratios than smaller habitats (MacArthur and Wilson, 1967), I hypothesize that this phenomenon may drown out competitive signals that are evident elsewhere in smaller seeps. We also found that smaller seeps were more likely to carry the most common species (*Mimulus guttatus*, *Triteleia peduncularis*, *Delphinium uliginosum*, see Table 1), whereas more rare species were more likely to occur in larger seeps. This may mean that there is a component of rarity that cannot be overlooked – it would be useful to analyze where rarely-occurring species fall within the color vision triangle of our focal pollinators. We could imagine that the rare species occupy the same color space of more common species such that they are filling in niche space as a lesser competitor. Alternatively, rare species could “escape” the normal color space created by



common species such that they are differentially stimulating photoreceptors – although at the loss of being less effective, but potentially avoiding heterospecific pollen transfer by being significantly different from the common species. With further experimentation in documenting species turnover, manipulation of seep communities (including species addition experiments), we can begin to clarify the pattern we observed of decreasing overdispersion with increasing components of seep size and diversity.

In conclusion, we have documented a trait pattern that to our knowledge has not been demonstrated in the literature over an entire co-occurring community without also being phylogenetically conserved or expressing phylogenetic community trait structure. We have also provided evidence that these observed plant communities could be responding to pollinators as selective forces in community assembly. Further studies should also consider exploring other members of the seep community (e.g., herbivores) to measure the impact each type of interaction may structure the ecological community. To come back to Levin's MacArthur Award lecture, it is important to recall, "communities are not well integrated units that move en masse ... there is no single correct scale or level at which to describe a system." Instead, we must find an appropriate balance of mechanistic considerations, patterns, and ecological scaling to understand the generation, maintenance, and restoration of ecological diversity in a rapidly changing world.

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